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The Effect of Temperature and Light on *Metrosideros polymorpha* Seed Germination[1]

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ABSTRACT: Seeds of a Hawaiian rain forest tree species, *Metrosideros polymorpha*, were germinated at temperatures ranging from 5 to 35°C and under photosynthetic photon flux densities ranging from 0 to approximately 2000 $\mu E \cdot m^{-2} \cdot s^{-1}$. Results after 30 days indicate that 25°C is the optimal temperature and 170 $\mu E \cdot m^{-2} \cdot s^{-1}$ or about 4–15 percent relative irradiance is the optimal light intensity for *Metrosideros* germination. Declining germination at higher irradiances was probably due to excessively high temperatures and intermittent desiccation. No seeds germinated at temperatures less than 12°C. Light was not found to be strictly required but improved germination by up to four times. Only 14 percent of the seeds sampled appeared to have intact embryos, hence the poor (15 percent) germination achieved even under optimal conditions.

Low temperatures (generally less than 17°C) must curtail germination success on the floor of montane rain forests. The higher temperatures associated with increased light intensity are probably more beneficial than light itself in increasing germination success in forest clearings. These relationships to light and temperature may partly explain why *Metrosideros* seedlings are often infrequent beneath dense rain forest canopies.

THE MOST COMMON CANOPY-FORMING tree species in the Hawaiian Islands is *Metrosideros polymorpha* Gaud. (Myrtaceae). Canopy dieback of this species on the island of Hawaii and the role of this phenomenon in stand maintenance is currently under investigation (Mueller-Dombois 1981). An assessment of the regeneration requirements of a species must consider the effects of environmental conditions on its germination success. This investigation specifically addresses the issue of optimal temperature and light conditions required for maximum germination of *Metrosideros* seeds.

On the island of Hawaii, *Metrosideros* can be found growing naturally from sea level to an elevation of 2700 m (9000 ft) (Rock 1913). This implies a range in annual mean air temperature from approximately 9 to 23°C (Doty and Mueller-Dombois 1966) and that *Metrosideros* must be able to germinate across this temperature range. It has been suggested that *Metrosideros* cannot maintain itself in mature rain forests due to the fact that its seedlings cannot become established in the dense forest shade (Mueller-Dombois et al. 1980). Corn (1979) states that light is required for the germination of this species. Sarvas (1950), Evenari (1964), Black (1969), and Toole (1973) cite many examples of species with seeds that do not germinate in the absence of light or for which germination success is increased by the presence of light.

Environmental conditions of light and tem-

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perature at the floor of the montane rain forest may thus not be optimal for *Metrosideros* germination. The experiments described in this paper investigate the roles of light and temperature in regulating *Metrosideros* seed germination.

MATERIALS AND METHODS

Seeds were gathered on 4 November 1979 from the half-opened capsules of a *Metrosideros polymorpha* tree (probably of the variety *incana*) at the end of 'I'iwi Road north of the village of Volcano on the island of Hawaii at an elevation of 1180 m. Five experiments were carried out, the first two in November 1979 and January 1980, and the remaining three in May 1980. *Metrosideros* seeds reportedly do not require any dormancy-breaking treatments, but start losing viability after several months (Corn 1979). Maximum percent germination was almost identical in both sets of experiments, so loss of seed viability was not considered to be critical.

Seeds were germinated on filter paper moistened with distilled water in 50-mm-diameter covered petri dishes. One hundred seeds chosen at random were placed in each dish and divided into four replicates of 25 seeds each. The number of plump (as opposed to shrivelled) seeds was counted in all samples.

Experiment 1: Germination at Different Temperatures

A temperature gradient of 5–35°C was established by a thermostat-controlled flow of heated and cooled water through the metal walls of a small cabinet. Temperatures along the gradient were measured with a thermocouple twice during the course of the experiment. One dish (with four replicates) was located at each of the following temperatures: 6, 12, 17, 22, 27, 32, and 35°C. Seeds were germinated in the dark except for about 5 min of illumination received every time germination counts were made; additional water was provided at this time if required.

Experiment 2: Germination at Different Irradiances and 20°C

Different light intensities were established by putting petri dishes at different distances from a bank of fluorescent lights. Dishes were kept in a growth room maintained at 20°C and received 16 hr of light daily. Light levels were measured in terms of photosynthetic photon flux density (PPFD), using a LI-COR LI-185A quantum flux meter. Single dishes received treatments of 0, 13, 22, 43, 133, and 211 $\mu E \cdot m^{-2} \cdot s^{-1}$ (where one Einstein, E, is Avogadro's number of photons).

In both experiments 1 and 2, the number of germinants in each replicate was counted with the aid of a stereo dissecting microscope at 5-day intervals for 4–5 weeks, after which no more germinants appeared. A seed was considered germinated when the emerging radicle was longer than it was wide.

Experiment 3: Germination at 10–30°C, *Continuous Light or Darkness*

This experiment was similar to experiment 1, but considered a narrower range of temperatures, had distinct light and dark treatments, and used more replicates. *Metrosideros* seeds were placed in growth rooms maintained at 10, 15, 20, 25, and 30°C. At each temperature, four petri dishes (16 replicates, 400 seeds) were placed under fluorescent lights and received 100 $\mu E \cdot m^{-2} \cdot s^{-1}$ of photosynthetically active radiation 24 hr a day. Another four dishes of seeds were kept in metal canisters under the same conditions and received no light.

Experiment 4: Germination under Fluctuating Temperature and Light

Metrosideros seeds were exposed to different levels of natural light (of greater intensity than could be produced by fluorescent lights) in a greenhouse and to the natural temperature changes associated with day and night and with altered irradiances. Light intensities were controlled by placing different numbers of layers of nylon shade cloth over

the experimental material. With no shade cloth, PPFD at noon varied from 260 to 2000 $\mu E \cdot m^{-2} \cdot s^{-1}$, depending on sky conditions. Because of this variability, light treatments are expressed in terms relative to light in the open and are only roughly comparable to the treatments used in experiment 2.

Relative irradiance levels are based on PPFD measurements taken at noon under clear, cloudy, and overcast conditions. With no shade cloth, light was considered to be 100 percent relative irradiance; temperatures generally ranged from 23 to 40°C daily. Under one layer of shade cloth, relative irradiance was 33 percent and temperatures ranged from 22 to 36°C. Under two layers of shade cloth, relative irradiance was 10 percent and temperatures ranged from 22 to 34°C. Three layers of shade cloth reduced light to 3.6 percent relative irradiance and temperatures ranged from 23 to 31°C. Four dishes of seeds (16 replicates, 400 seeds) were placed under each treatment, and another four dishes were kept in the dark in sealed canisters placed under three layers of shade cloth.

Experiment 5: Differentiation between Plump and Shrivelled Seeds

Two hundred seeds were selected visually for their plumpness and were germinated under one layer of shade cloth to determine whether they would germinate more successfully than a random sample of seeds.

In order to ward off fungal attack, seeds tested in the latter three experiments were immersed for 1 min in a 20 percent Chlorox solution (equivalent to a 1 percent solution of sodium hypochlorite), washed with distilled water, and transferred to presterilized petri dishes using sterile techniques. Distilled water was added daily to keep filter papers moist. However, the germinating seeds kept at 30°C and those kept in the darkened canisters at 25 and 30°C dried up at least once. Germination counts were made 30 days after the seeds were set out.

Average germination obtained in each experiment after 30 days was plotted against temperature or irradiance. The fit of these data to linear and polynomial expressions (to three terms) was tested by linear least squares regression methods. The significance of differences in responses brought about by the various treatments was evaluated by analysis of variance and Duncan's multiple range test.

RESULTS

Experiment 1: Germination at Different Temperatures

The rates of *Metrosideros* germination at different temperatures when kept mostly in the dark are shown in Figure 1. Greater germination was achieved at 32°C than at any other temperature tested, although seeds at 27°C initially showed the most rapid germination. No germination occurred at temperatures of 12°C or less, and germination at 35°C was also not very successful. The three-term polynomial equation that best fits ($R^2 = 0.91$) the plot of final germination against temperature (Figure 2) is $G = 6.1627 - 1.6621T + 0.1211T^2 - 0.0022T^3$, where G is percent germination after 30 days and T is the ambient temperature in degrees Celsius.

Experiment 2: Germination at Different Irradiances and 20°C

The rates of germination at different PPFD levels are shown in Figure 3. *Metrosideros* germination showed a generally positive response to increasing light levels, but the data exhibited a considerable amount of scatter. The equation fitted to the final germination data, portrayed in Figure 4 (line A), exhibits a positive response to light which levels off and then declines at higher irradiances. An alternative positive response is indicated by line B (Figure 4), with significantly higher germination achieved once a threshold light intensity of 100 $\mu E \cdot m^{-2} \cdot s^{-1}$ is reached.

Experiment 3: Germination at 10–30°C, *Continuous Light or Darkness*

The more controlled germination tests confirmed the general relationship to temperature found in experiment 1 and emphasized the

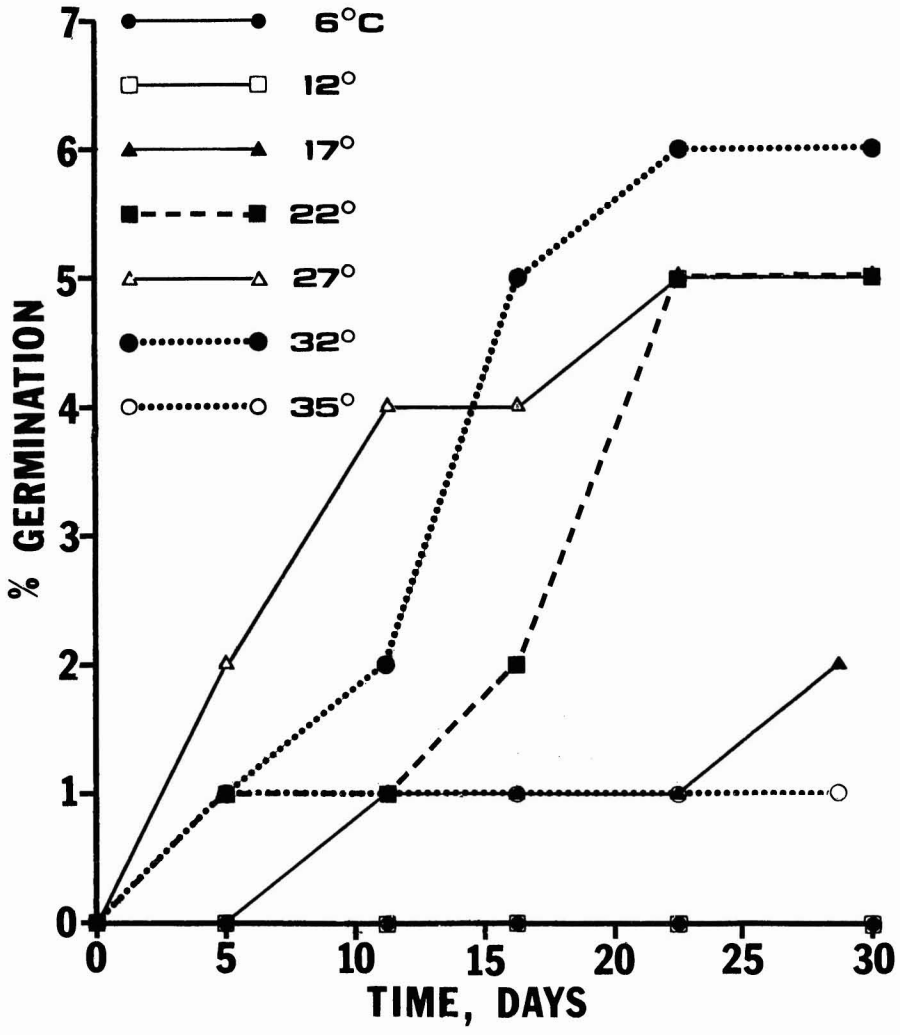

FIGURE 1. Progress of *Metrosideros polymorpha* seed germination at different temperatures (experiment 1).

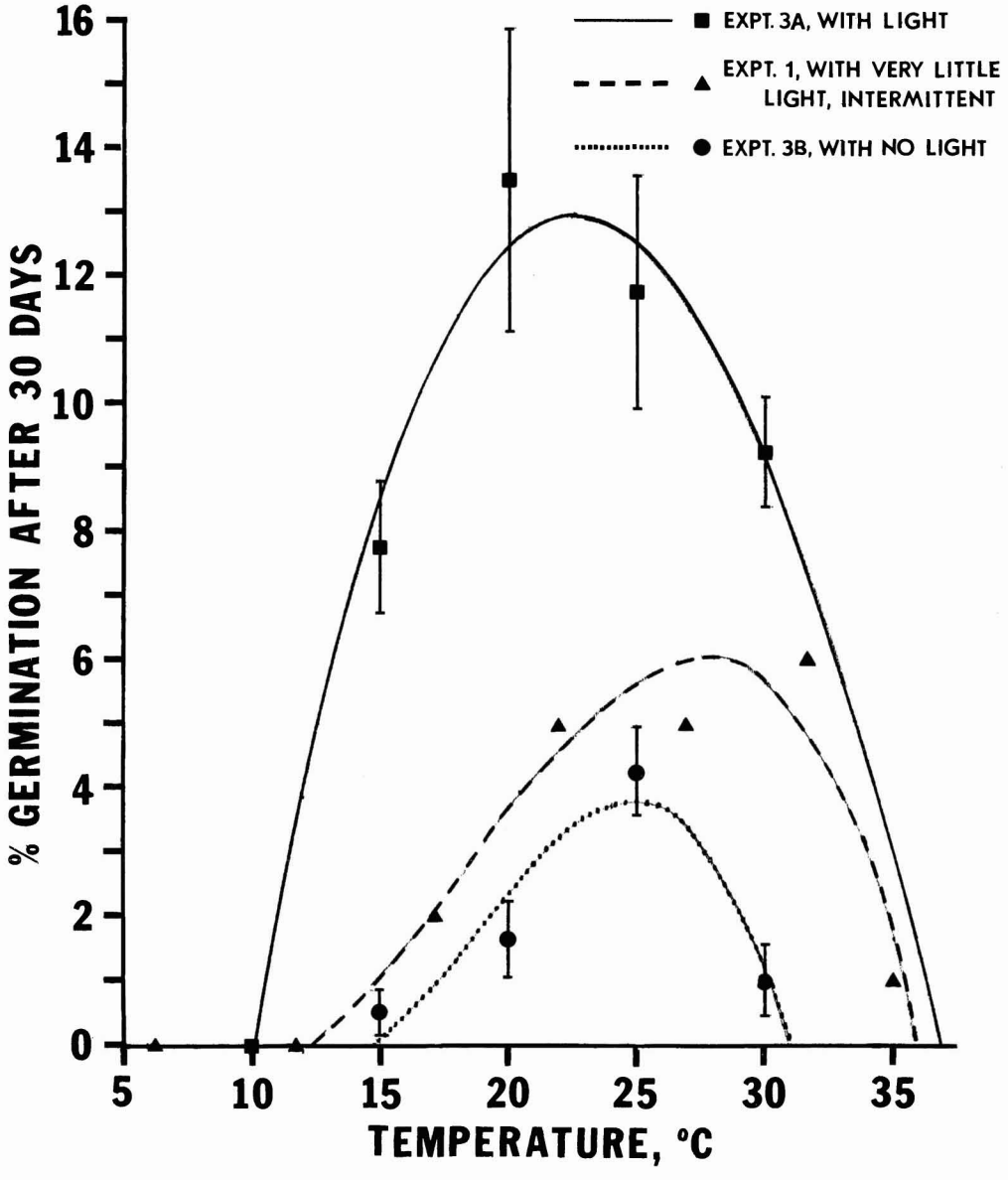

FIGURE 2. *Metrosideros* seed germination as a function of temperature with different amounts of light available. Experiment 3, vertical bars indicate ±1 SE. Experiment 1 standard errors are not shown here for the sake of clarity.

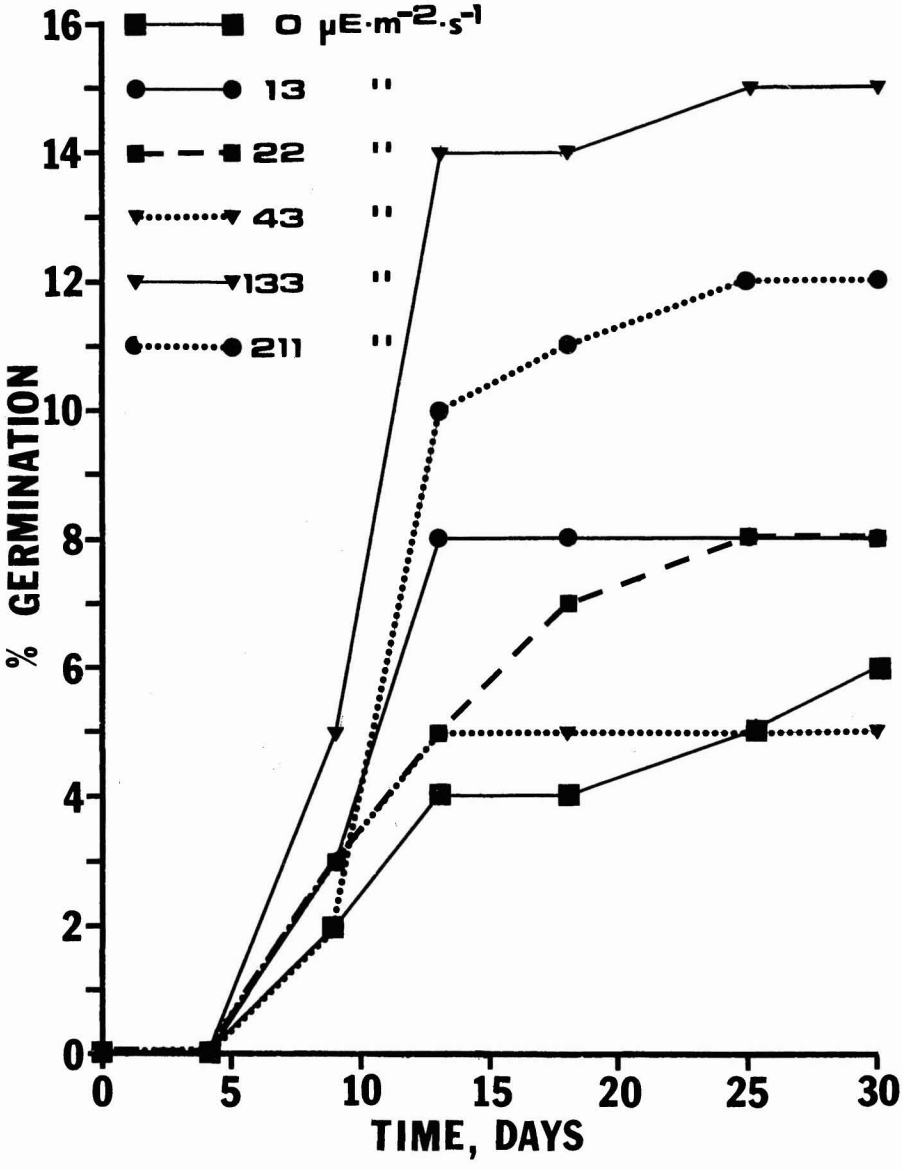

FIGURE 3. Progress of *Metrosideros* germination at different photosynthetic photon flux densities (experiment 2).

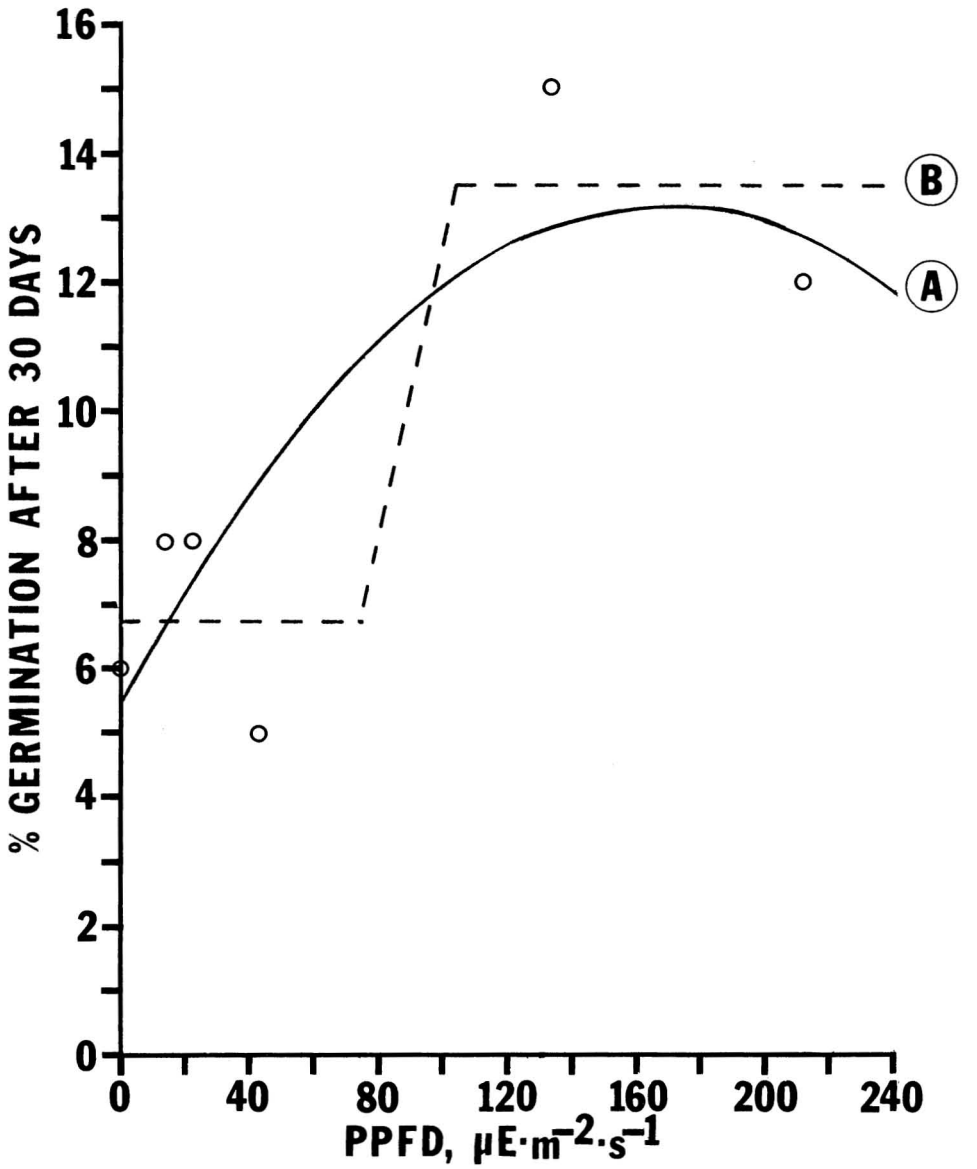

FIGURE 4. *Metrosideros* seed germination as a function of photosynthetic photon flux density (PPFD). Experiment 2, temperature is 20°C. Line A is a least squares regression model: $G = 5.4998 + 0.0913P - 0.003P^2$, $R^2 = 0.68$, where G is percent germination and P is PPFD. Line B is an alternative stepwise function based on a threshold model, joining the average germination response observed for PPFD above and below 100 $\mu E \cdot m^{-2} \cdot s^{-1}$.

different responses obtained under light and dark conditions (Figure 2). Germination at 25 and 20°C was significantly higher than at 30 and 15°C, which in turn was significantly higher than germination at 10°C. Germination was about three times more successful under constant illumination than in the dark, and interactions of light and temperature were also significant. The relationship of illuminated germination to temperature can be described by the equation $G = -33.8 + 4.5792T - 0.13T^2 + 0.0008T^3$ ($R^2 = 0.98$) and germination in the dark fits the equation $G = 20.466 - 4.0298T + 0.2428T^2 - 0.0043T^3$ ($R^2 = 0.91$), where G represents percent germination and T is temperature in degrees Celsius. Maximum germination is predicted to be at 23 and 25°C for light and dark germination, respectively.

Experiment 4: Germination under Fluctuating Temperature and Light

The greatest germination, 15 percent, was observed at 3.6 percent irradiance. Average germinations of 3.5, 8.2, 7.0, 5.0, and 0.2 percent were achieved at relative irradiances of 0, 3.6, 10, 33, and 100 percent full daylight, respectively. None of the linear or curvilinear equations tested could adequately describe these results, but the different germination responses were significantly attributable to the shading treatments tested. Data representative of additional irradiance levels would be desirable, but the findings are in general agreement with the results of experiment 2, where germination leveled off at the highest fluorescent light treatment (less than 10 percent full daylight). Results are further complicated by the fact that temperatures increased with light in this experiment, unlike in experiment 2. Consideration of the mean minimum and maximum temperatures characteristic of each shade treatment failed to explain any more of the data distribution when applied as secondary factor variables in a linear multiple regression.

Experiment 5: Differentiation between Plump and Shrivelled Seeds

Seed plumpness helps explain the generally low germination success achieved by *Metrosideros polymorpha*, as indicated by a sixfold difference in the germination of plump and random samples of seeds. Germination of 30 ± 3 percent was obtained for plump seeds in 30 days, as compared with 5.0 ± 1.0 percent success in a random sample of seeds kept under the same conditions. This is consistent with the fact that only 14 ± 1 percent of the *Metrosideros* seeds tested in this study were plump, based on 13 samples of 100 seeds each. That is, if only 30 percent of the plump seeds will germinate and plump seeds are only 14 percent of all seeds, then one would expect to see only 4.2 percent ($0.3 \times 0.14 = 0.042$) germination. This is within the confidence limits of the 5.0 percent germination observed in a random sample of seeds.

DISCUSSION

Characteristic of many physiological responses to environmental conditions, *Metrosideros* germination exhibits a parabolic relationship with temperature, being optimal at about 25°C and having less success in either direction to its tolerance limits at about 10 and 37°C. This agrees well with the mean annual temperatures that characterize the distributional range of *Metrosideros polymorpha*.

For temperatures of 22–32°C, the central or optimal range for germination, approximately the same final germination success is obtained, but is achieved more slowly at low temperatures. This observation indicates that a certain number of degree-days, or a particular level of total heat accumulation, is required for germination. Degree-day requirements simply reflect more rapid seed activation at higher temperatures, typical of the behavior of chemical reactions and a widespread feature of seed biology (Edwards 1932, Hegarty 1973, Koller 1972). This behavior is similar to the germination requirements of *Acacia koa*, another dominant Hawaiian rain forest tree species (Spatz 1973).

The relationship of germination to irradiance is a positive one, with a peak at intensities of approximately 170 $\mu E \cdot m^{-2} \cdot s^{-1}$. This result partly confirms Corn's (1979) assertion of the positive effect of light on *Metrosideros* germination. Zohar, Waisel, and Karshon (1975) report that light likewise has a beneficial effect

on the germination of *Eucalyptus occidentalis*, also a member of the Myrtaceae. However, the fact that significant germination occurs in the dark suggests that light is not strictly required. If light is a definite requirement, it is possible that this requirement could be met while seeds are inactive even though they receive no light after being imbibed with water. *Metrosideros* seeds never appear to be physiologically dormant or fully dehydrated under natural conditions and have thin seed coats, so they could conceivably be receptive to light before imbibation, especially under conditions of high relative humidity (Koller 1972).

Although germination is noticeably increased in the presence of light, the results of experiments 2 and 4 indicate that the effect is lost at high irradiances. This may be partly due to the effects of high temperatures; the 42°C temperature that developed under 100 percent relative irradiance is above the tolerance limits for *Metrosideros* germination as indicated by experiments 1 and 3.

Maximum germination occurs at higher temperatures when light is lacking. This phenomenon is illustrated in Figure 2, where the peaks of the derived regression lines are located at 3–6°C higher when germination occurred with little or no light as compared to continuous light. In contrast, *Eucalyptus* seeds exhibit more high-temperature germination in the light than in the dark (Zohar et al. 1975). The few data points used in the regression do not permit a statistical analysis to determine whether the derived curves peak at significantly different temperatures. If significant, it is possible that the activation of certain enzymes can be accelerated by either light or heat. A similar conclusion was reached by Toole (1973). To test this finding, it is hypothesized that more *Metrosideros* seedlings should be found in the deep shade of low-elevation forests (where temperatures are higher) than under the same light conditions at higher elevations.

The role of light in plant processes other than photosynthesis is usually by means of some phytochrome-mediated mechanism. Koller (1972) suggests that the capacity of a seed embryo to grow is a function of its content of active phytochrome. Activation of phytochrome-controlled mechanisms is generally considered a threshold process based on the amount of activated phytochrome, which in turn depends on a required amount of the appropriate waveband of light (Salisbury and Ross 1978, Smith 1973). As a result, a continuous positive relationship of germination to light intensity is not expected. However, closer inspection of Figure 4 and a Duncan's multiple range test of data from experiment 2 reveal that the responses to the four lowest light treatments represent a clustering of neutral responses, while germination success at 133 and 211 $\mu E \cdot m^{-2} \cdot s^{-1}$ indicates a significantly positive response. This is portrayed by the stepwise (threshold) relationship described by line B in Figure 4. In experiment 4, germination at all levels of irradiance greater than zero probably represent positive responses, but this response is nullified at the higher irradiance levels by temperatures too high for successful germination. It should be noted that no completely satisfactory explanation for the mechanism of phytochrome action has yet been proposed (Vidaver 1977).

Another factor that helps explain observed germination success is the plumpness of the seeds. When taken into account as a second factor variable in a multiple regression of germination on irradiance using results from experiment 2, seed plumpness helped explain 21 percent more of the data variation. (With a multiple R^2 of 0.72, the derived relationship is $G = -3.0633 + 0.0035P + 0.8343F$, where G is percent germination after 30 days, P is the PPFD of light, and F is the percentage of seeds that are filled or plump as opposed to shrivelled and empty.) It is logical that seed germination varies not only with environmental factors but also with the inherent viability characteristics of a particular seed sample.

The shrivelled seeds do not appear to be viable seeds at all, since they have no embryo. They are actually unfertilized ovules or some other infertile developmental product of the ovule. Dissection reveals that plump seeds contain an embryo that occupies most of the seed's volume and has easily distinguished cotyledons. The shrivelled seeds consist only of the outer seed coat or some combination of tissues probably derived from the nucellus and integuments. The difference between the two seed types is illustrated in Figure 5.

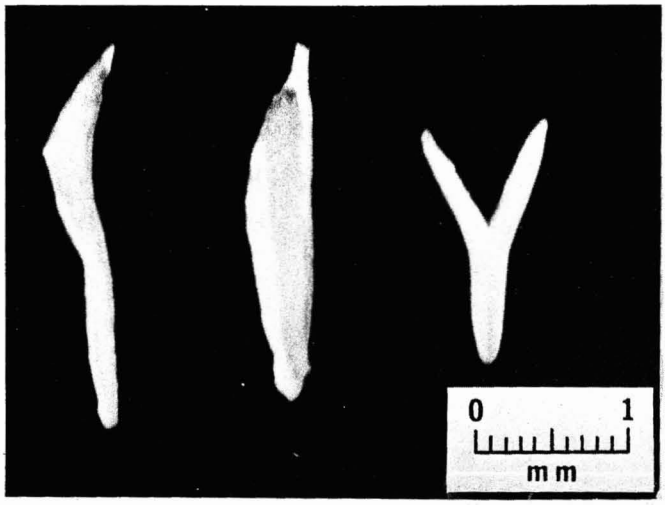

FIGURE 5. *Metrosideros polymorpha* seeds, showing the difference between unfilled and filled seeds. From left to right: shrivelled unfilled seed; plump filled seed; embryo dissected out of a plump seed (note cotyledons).

The high proportion of seeds that are infertile would seem to confirm Carpenter's (1976) claim that red-flowered *Metrosideros* trees are partially self-incompatible. However, the co-occurrence of plump and shrivelled seeds in the same capsules calls into question Carpenter's use of the number of mature capsules as an indicator of self-compatible or self-incompatible plants. Low overall seed viability may also be indicative of a paucity of suitable pollinators, notably the native Hawaiian honeycreeper species thought to have been the tree's major pollinators in the past.

Inadequate fertilization and outcrossing is not the only factor that could account for the presence of few embryos. Alternative explanations for the presence of shrivelled seeds include the possibility that some ovules are originally sterile, as reported for some species of *Adonis*, *Clematis*, and *Anemone* (Bhatnagar and Johri 1972). However, Dawson (1970) notes that the *Metrosideros collina* group (of which *M. polymorpha* is a member) as a whole has ovules that are all potentially fertile. Another consideration is that ovules, embryos, or entire flowers may abort if a plant is exposed to nutrient stress (Pollock and Roos 1972). Self-incompatibility remains the most likely explanation; fertile seeds are few and are randomly disposed in the capsules of most members of the *M. collina* group (Dawson 1970).

The observed response of *Metrosideros polymorpha* germination to temperature and light may help explain some of the difficulties this species encounters in maintaining its presence in montane rain forests. These forests are found from about 900 m (3000 ft) to 1700 m (5500 ft) elevation on the island of Hawaii, so that average air temperatures (approximately 18–14°C) are less than optimal for *Metrosideros* germination as indicated by this investigation. Soil temperatures measured near noon in the ʻŌlaʻa Tract rain forest for 14 days in the summer of 1979 averaged 16.5°C (Burton 1980). This is compared to 19.8°C found in the moss mats covering fallen tree fern (*Cibotium* spp.) logs, the preferred substrate for *Metrosideros* establishment in the montane rain forest. These warmer temperatures and the role of logs as refuge from flooding and damage by feral pigs may explain why tree fern logs contain most of the *Metrosideros* seedlings encountered. The question of substrate preferences in *Metrosideros* germination is considered in greater detail by Cooray (1982).

Average summertime soil temperatures in an artificial clearing in the ʻŌlaʻa Tract rain

forest were measured to be 19.2°C (Burton 1980). Seeds deposited in forest clearings or in open areas such as lava flows would therefore be expected to show greater germination success because temperatures are warmer than for those seeds situated beneath the cooling shade of a dense forest canopy, providing moisture is not limiting. This expectation has proven correct; more *Metrosideros* germinants appear during a given time interval if the forest canopy is opened or thinned than in an undisturbed forest (Burton 1980, 1981).

The positive influence of higher light intensities in openings would similarly ensure that a higher percentage of *Metrosideros* seeds germinate successfully. These responses partly explain why *Metrosideros polymorpha* behaves as a shade-intolerant species and why it may encounter difficulty in getting established in dense forests. Light may be somewhat of a limitation to seed germination on the forest floor. Although light is not strictly necessary for germination and optimal conditions for germination can be achieved at low irradiances, the relative irradiance at the floor of a montane rain forest (again in ʻŌlaʻa Tract) averages about 1.9 percent (Burton 1980). This is less than the 3.6 percent relative irradiance that supported the greatest germination in experiment 4.

The growth and success of seedlings in response to light and temperature are also important in explaining the differential success of *Metrosideros* regeneration under different conditions of overhead canopy density (Burton 1980), but the effect of these same environmental factors on germination cannot be overlooked.

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